Redescriptions of *Cystopelta petterdi* Tate, 1881 and *Cystopelta bicolor* Petterd and Hedley, 1909 (Pulmonata: Cystopeltidae)

by Ron C. Kershaw

Honorary Research Associate, Queen Victoria Museum, Launceston.

ABSTRACT

The Tasmanian terrestrial pulmonates *Cystopelta petterdi* Tate, 1881 and *Cystopelta bicolor* Petterd & Hedley, 1909 are redescribed and neotypes erected. A diagnosis of *Cystopelta* Tate, 1881 is provided.

INTRODUCTION

Two species of *Cystopelta* Tate, 1881 are recorded from Tasmania, *C. petterdi* Tate, 1881 and *C. bicolor* Petterd & Hedley, 1909. Due to the range of superficial variation identification of these species has been uncertain. No recognizable type material is known although dried possible syntype specimens of *C. bicolor* exist in the Australian Museum and the Queen Victoria Museum. This material does not constitute effective type material (B.J. Smith, pers. comm.).

This paper describes the anatomy of *C. petterdi* and *C. bicolor*, erects neotypes and provides a diagnosis of the genus *Cystopelta*. Tate's (1881) description of the genus clearly established the external appearance of a shell-less animal with a distinct visceral mass protected by an "inflated or bladder-like shield". This shield is apparently a modification of the mantle and possibly lappetts now indistinguishable. The animal is a semi-slug as defined by Tillier (1984).

THE FAMILY

The first record of a family name is that of Cockerel (1891) who introduced Cystopeltinae on the basis of narrow teeth and "ribbed jaw". The "ribs" are in fact folds. Iredale (1937) gave the group family status and this was accepted by Kershaw (1955), McMichael & Iredale (1959), Altena & Smith (1975), Smith (1977, 1979), Smith & Kershaw (1979, 1981) and Bishop (1981). Cystopeltinae was used by Thiele (1931), Baker (1956), Zilch (1960) and Burch (1976).

These decisions on family status were based on anatomical studies by Hedley (1890b) and Davies (1912) dealing with material from New South Wales and Victoria. Hedley later (1891) remarked that he could not separate Mt Kosciusko and Launceston specimens he dissected. Thiele's (1931)

description was based on radula and genital data. The family is more complex than anticipated and definition is beyond the scope of this paper which continues studies previously briefly reported (Kershaw, 1957). The work suggests a possible second genus in Tasmania.

The Cystopeltidae are endemic to eastern Australia from southern Queensland to Tasmania. Brief descriptions and distributional data are provided by Smith & Kershaw (1981). Bishop (1981) referred to food and habitat. Recognition of the species level taxa of Davies (1912) and Iredale (1937) was delayed by Smith & Kershaw (1979, 1981) due to the need for authentic material from Tasmanian type localities.

MATERIAL AND METHODS

The neotypes proposed in this paper are lodged in the Tasmanian Museum. This study is based on material lodged in the Tasmanian Museum (TM), the Museum of Victoria (NMV), the Queen Victoria Museum (QVM) and the author's collection to be lodged in these museums. Voucher material is lodged in these museums and the Australian Museum (AM) Sydney.

Grid references provided refer to the 1:100 000 Topographic Survey, Tasmania, Sheet 8315 (St Patricks), 8015 (Hellyer) and 7915 (Arthur River). All dissections were done by the author using either a Zeiss or a Wild dissecting microscope with drawing attachment. Drawings and photographs are by the author. Scanning electron micrographs of the radulae are by Adrian Daniell of La Trobe University.

Material dissected includes 40 specimens of *C. petterdi* together with many others from Tasmanian and Victorian localities. Only three specimens of *C. bicolor* from the type locality vicinity and at least one from central Tasmania have been available for dissection. Similar animals not dissected occur in Victoria.

The nomenclature used for the genitalia in this study is based on that adopted by Tompa (1984).

CYSTOPELTA TATE, 1881

Type species by monotypy, *Cystopelta petterdi* Tate, 1881. Diagnosis: Semi-slugs in which the shell may be absent but is usually reduced to a thin horny membrane adhering to the distinct visceral hump enclosed beneath a flexible wrinkled mantle-shield below which the foot protrudes noticeably only in the crawling animal. A pedal groove (Fig.4) is clearly visible above the wide vertically lobed or almost smooth sole margin. There is no dart sac, penial verge, flagellum or caecum but an epiphallus is present. The atrium is elongate with an internal coiled duct fused to the atrial wall. The oviducal pore within the vagina (Figs.12 and 18) is a variably prominent cone shaped process which is extrudable and possibly has a stimulatory function. The genitalia are extruded during copulation.

The relatively short tail (Figs.4, 5 and 16) is truncate and recessed with a distinct caudal gland surmounted by a caudal horn above which is a small diamond shaped process. The short foot cavity which has the posterior margin anterior to the stomach, contains the anterior oesophagus and salivary glands overlapping the basal gonoduct lobe. The tentacle and buccal retractors insert with a reduced columellar muscle above the posterior margin. The right ocular tentacle passes above the vagina (Fig.16)

The jaw (Fig.6) is very thin, flexible, capable of small folds and transversely marked by very fine very close lirae variably visible cut by faint longitudinal striae.

The radular teeth (Figs.20-33) are mounted on very long narrow basal plates. The central tooth is unicuspid or tricuspid with lateral cusps markedly anterior to the elongate median cusp. The lateral teeth are tricuspid or multicuspid. The marginal teeth are multicuspid and become more elongate narrow with the cusps of outer marginals more or less prominent elongate.

Generic features

The conspicuous oviducal cone-shaped papilla observed in the vagina, here termed an-

'ovipositor' (Figs.12 and 18) is believed confined to this genus. It is distinct from the inconspicuous pore papilla of certain other animals. Mating observations supported by those of Daniell (in litt., 1985) suggest that the organ has a role during copulation. The genitalia are extruded during copulation, the parts involved depending on the role of the individual animal as male or female. The atrium upon extrusion forms a flexible sheath, the 'atrial sheath'. The contained coiled duct, here termed the 'atrial duct', straightens with extrusion but remains within the sheath. Another example of genital extrusion in the case of *Partula affinis* Pease was described by Kondo & Burch (1979).

Evolution toward slug morphology has resulted in modification of superficial form as well as anatomy so that convergence tends to restrict factors of taxonomic value. However the genitalia display features which have species, generic and family value. In *Cystopelta* the prominent vaginal papilla and the fusion of the atrial duct at the gonopore and internally are here considered diagnostic features. A distinct group exists in which the oviducal papilla is greatly reduced and the atrial duct is only partly fused or not fused. These components are not continuous with the vaginal and penial chambers as in typical *Cystopelta*.

Suprageneric features

The foot structure and kidney structure places the animal in the Aulacopoda Sigmurethra (Pilsbry, 1946; Solem, 1959) although the ureter is much modified and the writer cannot distinguish a secondary component. The primary ureter is a distinct duct curving from the apex postero-dorsally (Fig.7) (Davies, 1912) across the kidney into the pneumostome chamber adjacent to the anus and pneumopore. On the basis of radula factors the animal belongs to the Limacacea (Solem, 1959; 1978). The globular ovotestis has subcylindrical component lobules radiating from the central ovotestis duct (Fig.9) to be capped externally with white distinct apices. The gonoduct is distinguished to a significant degree by a structural division into apical and basal lobes from which the oviduct and vas deferens branch as usual (Figs.11 and 17). The apical lobe contains a capacious lumen across which the path of the uterus appears curved (Fig.13). At first this was considered distinct from the male duct but further observation has revealed a fairly brief region of commonality. The basal lobe is a complex of elements which appear discrete but the degree to which the ducts are common or separate must await study at the family level.

Relationships

There is no clear association with Australian genera studied as yet. The marginal teeth suggest a relationship to the helicarionid snails which appears less apparent in Tasmanian *Helicarion* (Dartnall & Kershaw, 1978; Kershaw, 1979). Urocyclid forms (Solem & Van Goethem, 1974) do suggest that marginal teeth denticles should be considered. The series of cusps present on *C. bicolor* marginals may indicate a common ancestral form for *Cystopelta* and an helicarionid assuming that in the latter the marginal cusps have modified. But this is no more than supposition.

Hedley (1890a; 1890b) and Iredale both suggest a resemblance to *Helicarion* and further comparisons can be made in tooth number (Solem, 1976). Comparisons can be made with genera of the Euconulidae (Baker, 1941) or the Microcystinae (Baker, 1938) in the presence of an epiphallus with no flagellum, a caudal foss and horn and a simple spermatophore. However there are also resemblances with the Arionacea when comparisons are made on the basis of the work of Solem (1982) especially in the epiphallus structure (Climo, in litt., 1986) in the Charopidae.

CYSTOPELTA PETTERDI TATE, 1881

Neotype: One specimen TM E16318 (Figs.1 and 2) collected by A. Daniell and R.C. Kershaw, 21 May 1984, 1 kilometre west of Cataract Gorge near Launceston, Tasmania, grid 508800mE 5411650mN about 100 metres above sea level.

Description

External: The animal (Fig.1) of medium size is 37mm long reaching to about 40mm fully extended. The mantle-shield is variously coloured brown to dark brown or greyish with mottles and often lines on the flanks. The whole fades to greyish shades with the shield contracting in preservative

(Fig.2). The body is pale grey to off white but the foot margin and tail may be brownish, bluish or grey. The upper tail ornament is a tubercular surface defined into a chevron pattern accentuated by brown lines separating the dense mottle of minute pale spots also present on the shield.

Anatomy

The jaw (Fig.6) is yellow, very thin and flexible and often variably crumpled into small folds.

The radula (Fig.20) of about 96 rows of minute teeth has some 400 teeth per row. The teeth are narrow elongate and are mounted anteriorly on elongate basal plates. There are about 25 or 26 lateral teeth which appear to grade into the marginals but variation is present.

The central tooth (Fig.21) is strongly hooked unicuspid, the long cusp having a scalloped curve to the basal plate which is narrowed at its extremities, strongly buttressed below the hook and laterally tapered outward. Anteriorly the plate is short and slightly hooked, posteriorly it is elongate. The first lateral teeth (Fig.21) are tricuspid with a rather narrow pointed very elongate mesocone, a much narrower endocone reaching to about mid-point and a short anterior ectocone. The stump of a possible second ectocone can be seen on one tooth. Clearly longer than the central tooth these teeth are laterally angled and curved upward posteriorly.

The subsequent laterals (Figs.22 and 23) have the same pattern but there is an added elongate narrow endoconal cusp on some teeth between the prominent endocone and the mesocone, which varies in apparent length. This cusp becomes longer and stouter than in earlier laterals. Viewed laterally the mesocones are seen to be hooked and the endocones extend more than half the tooth length. The cusps are elongate and pointed when free of wear. Mostly there is one clear long ectocone but there are stubs of a second.

The transition (Figs.24 and 25) to the marginals is not precise but the second endocone becomes more prominent and a second ectocone bolder more frequent. This is noticeable near an aberrant tooth (Fig.25), no more than a stump with one cusp about one third the distance from the central tooth. Here most teeth have one long ectocone. The viewing angle to the right reveals the sides of the plates. The second ectocone is more commonly visible. The marginal teeth (Fig.26) have two elongate ectocones and the endocones are more elongate although variable. The outer endocone is distinctly prominent and almost as long as the mesocone. The basal plates appear narrower more elongate.

Variation is indicated between the several radulae studied. A feature is the interrow junction which is prominent and raised like rope (Fig.23) in some areas or ridged (Fig.22) but may be barely prominent (Fig.21). In one case the teeth are strongly worn but the plate structure is clear and the elongate central tooth is almost hidden by the laterals.

Reproductive anatomy

Apical genitalia (Figs.11 and 13): The globular ovotestis is pale cream in colour tending to brownish in mature animals. The short hermaphroditic duct is enclosed within a thin transparent sheath and becomes kinked with the development of seminal vesicles. It enters the somewhat sub-ovoid shaped albumen gland laterally to junction with the talon below the surface. The talon (Fig.13) is about 1 mm long with a distinct apical lobe usually just protruding from the albumen gland surface. The talon narrows sharply to the carrefour (Fig.13) which is narrow transverse then sharply angled into the oviduct-prostate junction. The oviduct enters the apical lobe of the uterus as a pale distinct duct initially apparently distinct from the prostate. The ducts become common briefly prior to the inter-lobe neck. The uterine lobe expands and becomes somewhat translucent with female sexual maturity but retains its globular shape. The basal lobe barely expands but also changes colour. The prostate (Fig.11) is very pale cream barely visible in immature animals but becomes clear, wider and a deeper cream colour with male maturity. It empties to the vas deferens within the basal lobe.

Terminal Genitalia: The free oviduct (Fig.11) is either attached to or separate from the vas deferens at the point of bifurcation at the basal gonoduct lobe. It passes across the bursa duct opposite to the vas deferens as a narrow duct of 7 to 9mm length to the oviducal pore without discernable glandular tissue. The pore enters a swollen lumen within the cone-shaped ovipositor which consists

of a sleeve of 'skin' fused to the vagina wall apically and having a concertina like structure of ridges providing for expansion when extruded through the atrium and atrial duct. The vagina (Fig.12) is a swollen chamber some 3mm long resting almost transversely above the atrium and opening opposite the bursa duct pore.

The vas deferens (Figs.11 and 12) is a thin coiled duct about 9 to 12mm long passing across the bursa duct surface before expanding into the epiphallus which is a short but variable section of the duct expanding to the male pore. Internally the epiphallus is lined with two bold high narrow white pilasters with a narrow low pilaster between (Fig.12). There are very fine irregular low lateral ridges. The structure passes basally into very low ridges cut by transverse grooves within a briefly expanded section which narrows then expands into a vestibular area lined with subrounded pustules which narrows abruptly into the male pore situate adjacent the penial retractor attachment to the penial chamber.

The penial chamber (Figs.11 and 12) is a cylindrical lumen with or without an obvious rounded external swelling adjacent the retractor, capacious and weakly lined with longitudinal grooves and faint close ridges. Apically a variably ornamented and swollen process (Fig.12) is situated on the wall and when fully expanded is responsible for the external swelling. This process adjacent the male pore may have a stimulatory and/or diverticular function as the internal pouch may be filled with breakdown material such as occurs in the bursa duct lumen. Variations in the structure of the pore region have been seen. The penial retractor (Figs.11 and 12) is a short strong white tubular muscle arising from the ventral lung epithelium on the left side (Fig.5), attached to muscular epithelium from the bursa duct and then passing to the apical penial chamber surface broadly but superficially.

The bursa copulatrix (Fig.11) is a small globular body separated from its duct by a constricted narrow hiatus through the foot diaphragm which also constricts the neck between the two uterine lobes. The muscular epithelium to the penial retractor attaches at this point and is part of the diaphragm tissue enabling the retractor to control both penial and bursa activity. The bursa duct is capacious, weakly lined basally and receives spermatophore from which very little reaches the weak copulatrix. A spermatophore has been observed protruding from the pore into the penial chamber.

The spermatophore (Fig.8) is a yellowish transparent 6mm long capsule obtusely truncate anteriorly, curving to a fine point posteriorly.

The atrium is an elongate pouch opening at the gonopore, which contains the coiled atrial duct (Figs.10, 11 and 12) and is extruded as an atrial sheath containing the duct during copulation. The atrial duct is lined with many (about 36) very fine ridged folds which are continuous with the basal penial and vaginal chambers. The ornament is very variable and may be weak or clear but is often seen as a series of major folds with several minor folds between. The sheath normally protrudes following preservation.

The type locality

The type locality was identified by Hedley (1891) who collected there with Petterd. The neotype site is about a kilometre away due to suburban development. The site and habitat will be described elsewhere (Kershaw, ms.). Voucher material: One specimen AM C147139 collected A. Daniell and R.C. Kershaw, 21 May, 1984; two specimens QVM442 1985/8/1 (whole), QVM443 1985/9/2 (dissected) collected R.C. Kershaw 28 October, 1984, all from the neotype locality. Two specimens NMV F52162 and one specimen (dissected) NMV F52163 collected R.C. Kershaw 16 August, 1975 from adjacent the neotype locality, grid 508900mE 5411600mN.

CYSTOPELTA BICOLOR PETTERD & HEDLEY, 1909

Neotype: One specimen TM E16804 (Fig.3) collected R.C. & W.M. Kershaw, 7 Jun 986, adjacent road to Magnet Mine, west of Waratah, western Tasmania, grid 370400mE 541090 mN about 500 metres above sea level.

Description

External: The animal (Fig.3) of medium size is 33mm long. The mantle-shield is brown with grey brown patches mainly on the flanks and is produced posteriorly. The foot is dull green in life fading to pale cream in preservative, the head almost white and the tentacles pale cream. The neck is marked with shallow transverse grooves. The tail surface pattern of tubercles and grooves arranged as a chevron is barely accentuated. The sole margin is variably weakly lobed. The caudal mucus is green.

Anatomy

The jaw is very thin as in *C. petterdi* but coloured white on the upper arch surface, cream centrally and brownish on the lower margin.

The radula (Fig.28) curves to a shallow 'V' centrally. There are at least 300 minute narrow elongate teeth mounted posteriorly on elongate basal plates. Centrally about three fifths of the plate are anterior to the tooth but a gradual change occurs towards the margins revealing more of the plate posteriorly. The plate length increases slightly at first then the plates curve and twist in the transitional area so that the typical pattern is derived. Anteriorly the tooth arises from the plate as a very thin ridge expanding into the elongate mesocone.

The central tooth (Fig.29) is tricuspid with a minute denticle adjacent the elongate ectocones. The mesocone is elongate and barely or not hooked. The lateral teeth (Fig.30) are multicuspid with a relatively broad elongate mesocone, 2 or 3 endocones and 2 or 3 ectocones. The ectocones decrease in size to a very small cusp anteriorly. The outermost endocone is prominent. Four cusps sometimes appear or only one, possibly due to wear. There are about 50 lateral teeth to the transitional region where the plates become narrow and curve anteriorly.

The latero-marginal teeth (Fig.31) are distinctly smaller with the plates progressively curving and twisting anteriorly with an increasing proportion of the plate appearing posteriorly. The mesocone is short and narrow with 2 prominent endocones and 3 or 4 ectocones.

The marginal teeth (Figs.32 and 33) are much narrower and shorter with the mesocone about half the length of that of the laterals reducing to about one-third at the radula margin. The mesocone has become distinctly hooked (Fig.33). There are similar endocones arranged adjacent to the mesocone and 4 or 5 ectocones in a series anteriorly. The proportion of the basal plate now visible is obvious while anteriorly the plate is strongly twisted. (Fig.33).

Reproductive anatomy

Apical genitalia (FIgs.14 and 17): The globular ovotestis is small greyish pale cream. The albumen gland is large and pale orange. The apical lobe of the talon does not protrude from the surface of the gland. The talon is 0.9mm long, white in colour and enters the carrefour through a relatively elongate narrow duct. The carrefour is large, somewhat elongate, barely transverse and almost obtusely angled into the oviduct-prostate junction (Fig.14). The oviduct expands to enter the apical uterine lobe which is swollen and somewhat translucent with a large flattened internal lumen. The prostate (Fig.14) is white in the Magnet animal and pale cream in an animal from the Murchison Highway.

Terminal genitalia (Fig.17): There is a superficial resemblance to *C. petterdi* but the free oviduct is longer, about 10 mm or more. The vagina (Figs.17 and 18) is a swollen, short, 2mm chamber resting at a slight angle clearly above the atrium and opening distinctly above the bursa duct pore. The ovipositor (Fig.18) closely resembles that of *C. petterdi* although smaller in the animals dissected.

The vas deferens (Fig.17) is a thin short coiled duct 5.5 to 6.5mm long which passes across the bursa duct surface opposite the free oviduct and expands rather abruptly into the strongly expanded transparent epiphallus which joins the penial chamber laterally. Internally the epiphallus ornament is of 4 strong pilasters occupying most of the lumen with a very short lateral pilaster and traces of transverse ridges adjacent the male pore (Fig.18). The pore opens into a small pustular lined chamber from which the penial chamber opens over a distinct ridge.

The penial chamber (Fig.18 and 19) is cylindrical short and narrow without an internal or external swollen process adjacent the pore. It is lined variably with transverse and longitudinal fine ridges,

most complex near the bursa duct pore, which pass into the atrium and vagina. The penial retractor (Figs.16, 17 and 18) is a thin white muscle 3 to 4.5mm long arising from the lung diaphragm well to the left side near the heart. It appears to have no connection to the bursa duct and passes to the apical penial chamber in the male pore region.

The bursa copulatrix (Fig.17) is small with a constricted neck to its duct as in *C. petterdi.* The neck is attached to the foot diaphragm epithelium. The duct is capacious and enters the atrium at the base of the penial chamber but in this animal the atrium appears very shallow on the male side with little significant space between the pore and gonoduct site.

The spermatophore (Figs.15 and 19) is small, white and only slightly narrowed posteriorly. It was found protruding through the male pore (Fig.19).

The type locality

Petterd & Hedley (1909) state that the habitat is the Magnet Range and the Upper Pieman River. The type locality is here restricted to the Magnet area. The site and habitat will be defined and described elsewhere (Kershaw,ms.). *Cystopelta bicolor* is a rainforest species.

Possible syntype material: Two dried specimens AM C27807. One dried specimen QVM409 1983/9/4.

Voucher material: Three specimens collected R.C. & W.M. Kershaw all dissected. One specimen QVM427 1986/9/30 collected at neotype locality. Two specimens QVM428 1986/9/31 a and b collected 9 June, 1986 adjacent the Murchison Highway north of Hellyer Gorge, grid 382600mE 5430600mN, in coils of bark, rainforest north of neotype locality.

Remarks

The specimens from near the type locality are very uniform in appearance. Two specimens from central Tasmania had a brighter green foot as stated by Petterd & Hedley (1909) for their material. Of the four specimens dissected three are considered adult and two of these are from or close to the type locality. Most other forms of *Cystopelta* vary in colour a good deal but animals with a green foot are not often seen in Tasmania.

The most significant features distinguishing *C. bicolor* excluding the foot colour, are the radula and the terminal genital features. Evidence from the range of forms so far studied support the weight given here.

Species comparison

	C. petterdi	*C. bicolor*
Radular teeth:		
Central	monocuspid	tricuspid
Lateral	most tricuspid	usually 4 cusps
Marginal	2 ectocones	4-5 ectocones
Endocones	unequal	equal
Basal plates	not twisted	twisted
Jaw	yellow	white
Foot		
Margin	lobed	barely lobed
Colour	not green	green
Mucus	yellow green	green
Apical genitalia:		
Carrefour	immersed	bulging
Talon-carrefour	short	long
Carrefour-uterus	acute	obtuse
Terminal genitalia:		
Free oviduct	short	long
Vas deferens	long	short
Epiphallus	3 pilasters	4 pilasters

Epiphallus-penis	apical	lateral
Vagina-bursa duct	opposite	not opposite
Penial process	present	absent
Atrial duct	folds thin	folds bold
	not lined	lined
Spermatophore	tapered	barely tapered
Retractor muscle	thick	thin

The penial retractor of *C. bicolor* arises distinctly nearer the left flank than that of *C. petterdi.*

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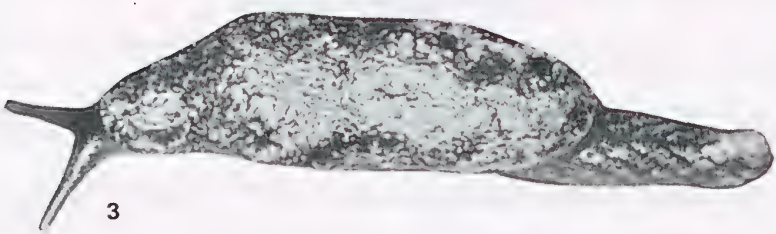

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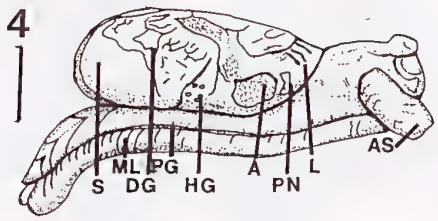
FIGURE 1. *Cystopelta petterdi* Tate. Neotype. Live length 37mm. FIGURE 2. *Cystopelta petterdi* Tate. Neotype preserved 26mm. FIGURE 3. *Cystopelta bicolor* Petterd & Hedley. Neotype. Live length 33mm.



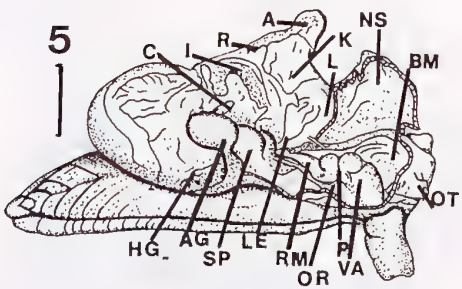
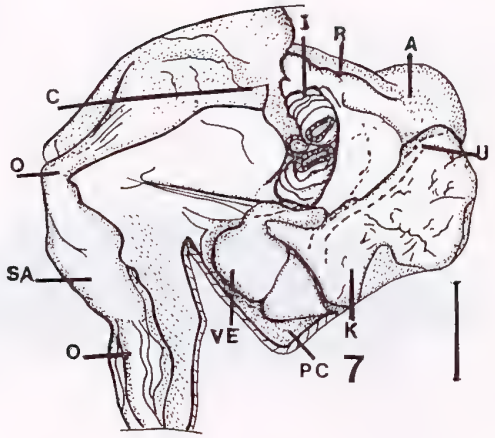
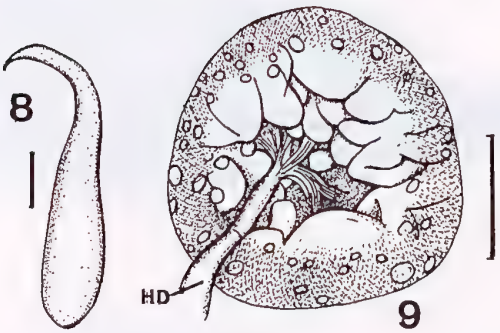


FIGURE 4. *C. petterdi*: lateral aspect of animal with shield removed. Scale line 5mm.
FIGURE 5. *C. petterdi*: partly dissected showing ventral aspect of pallial organs and foot organs *in situ*. Scale line 5mm.
FIGURE 6. *C. petterdi:* jaw. Scale line 1mm.





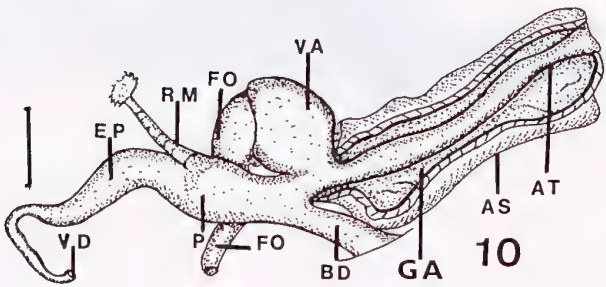
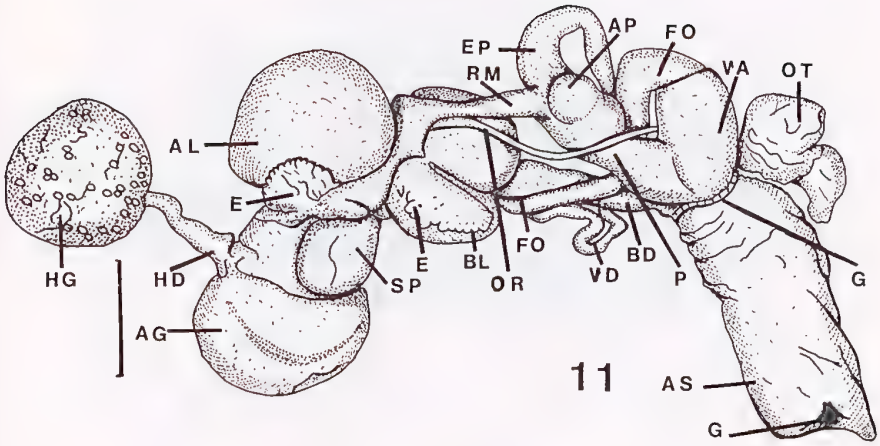


FIGURE 7. *C. petterdi:* Kidney (K), pericardium (PC), intestine (I) coils cut and salivary gland (SA) exposed. Scale line 2mm.
FIGURE 8. *C. petterdi*: spermatophore. Scale line 1mm.
FIGURE 9. *C. petterdi*: ovotestis internal structure. Scale line 1mm.
FIGURE 10. *C. petterdi*: atrial sheath (AS) opened exposing atrial duct (AT). Scale line 2mm.



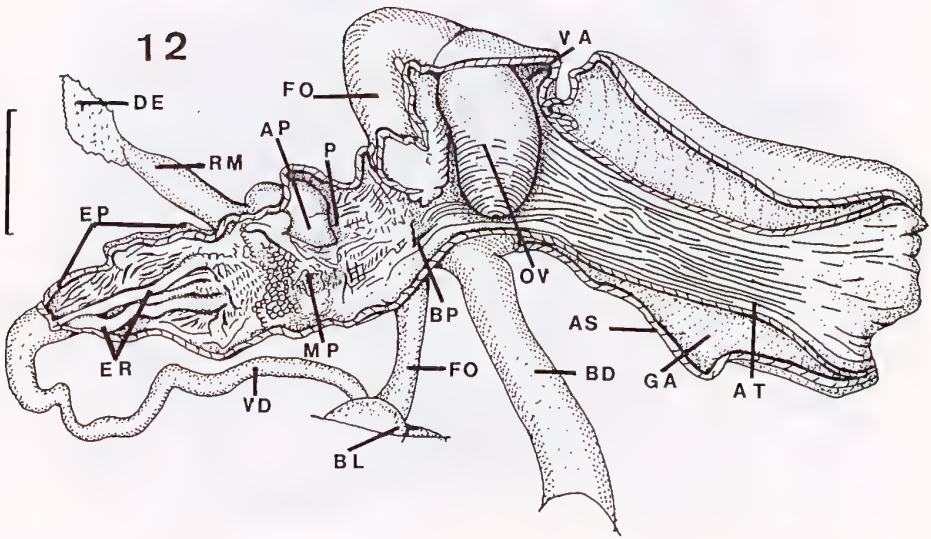
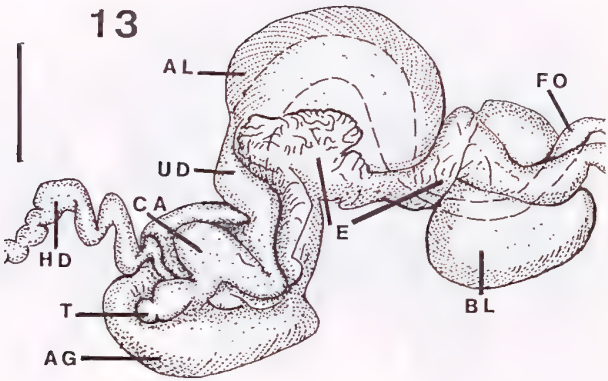


FIGURE 11. *C. petterdi*: genitalia as lifted from body of animal. Scale line 3mm.
FIGURE 12. *C. petterdi*: internal detail of terminal genitalia showing atrial duct (AT), ovipositor (OV), penial chamber (P), male pore (MP) and structure of epiphallus (ER). Scale line 2mm.



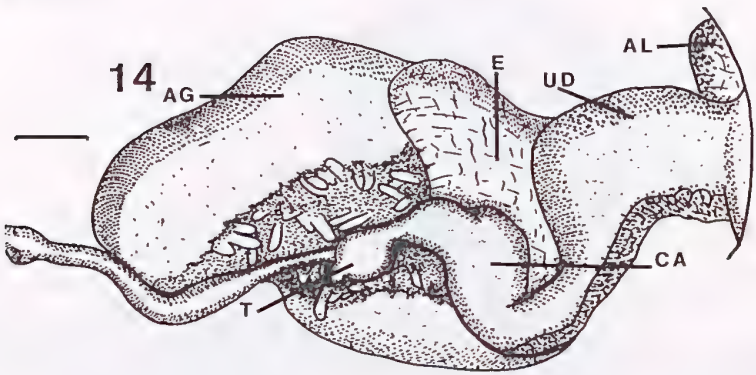
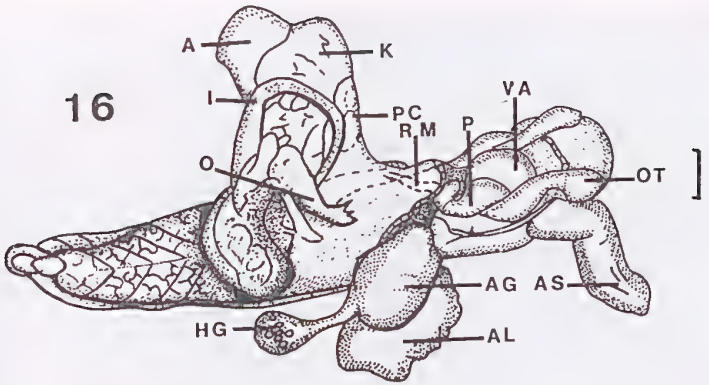


FIGURE 13. *C. petterdi*: apical genitalia showing relationship between talon (T), carrefour (CA), oviduct (UD), prostate(E) and lobes of uterus (AL,BL). Scale line 2mm.
FIGURE 14. *C. bicolor*: apical genitalia showing relationships between talon (T), carrefour (CA), oviduct (UD), prostate (E) and apical lobe (AL) of uterus. Scale line 1mm.
FIGURE 15. *C. bicolor*: spermatophore. Scale line 1mm.



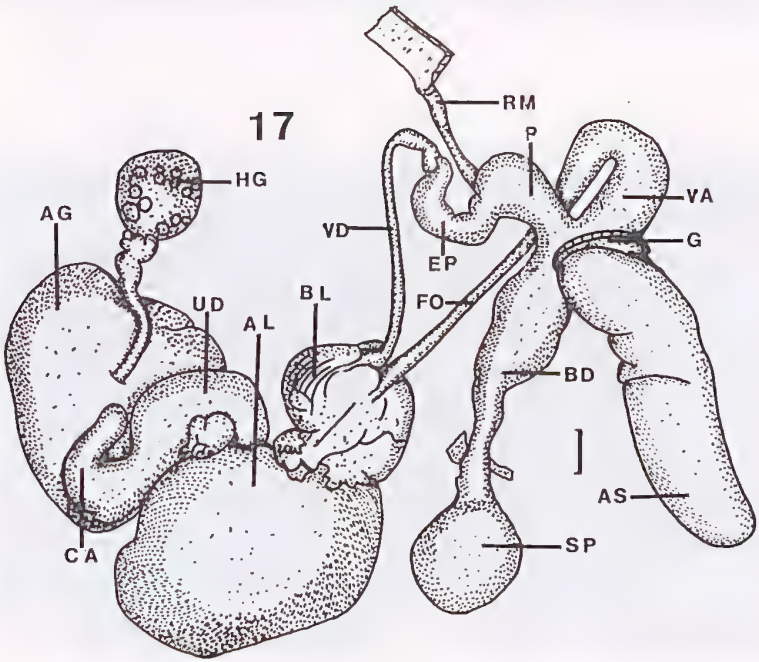
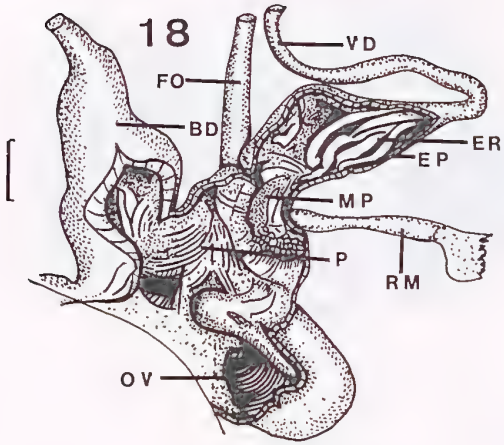


FIGURE 16. *C. bicolor*: animal partly dissected showing ventral pallial organs, path of penial retractor (RM) and optical tentacle (OT). Scale line 2mm.
FIGURE 17. *C. bicolor*: genitalia set out for dissection showing proportions. Scale line 1mm.



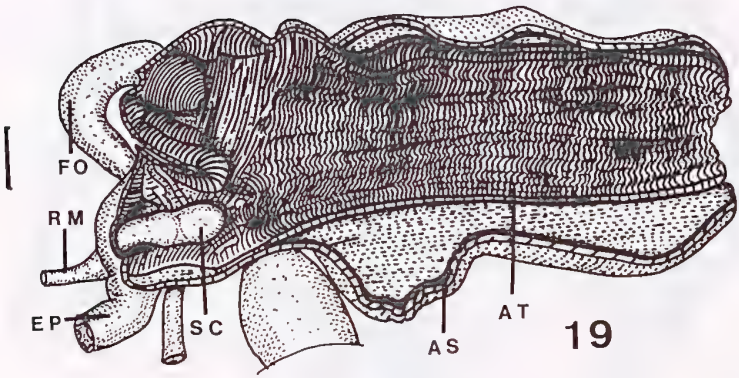


FIGURE 18. *C. bicolor*: internal structure of epiphallus (EP), penial chamber (P), male pore (MP), bursa duct (BD) pore and ovipositor (OV). Scale line 1mm.
FIGURE 19. *C. bicolor*: internal detail of atrial duct (AT) and vagina (VA) with spermatophore (SC) protruding from epiphallus (EP). Scale line 1mm.

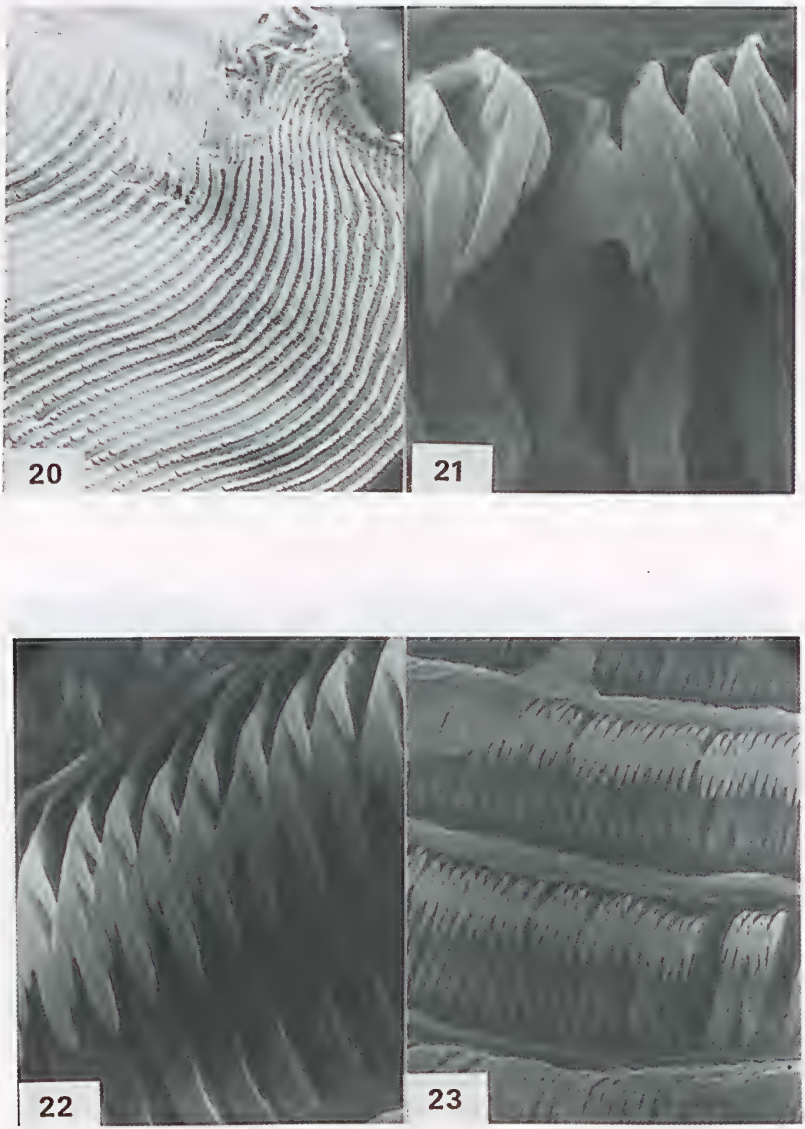


FIGURE 20. *C. petterdi*: radular teeth at X50.
FIGURE 21. *C. petterdi*: central and adjacent lateral teeth at X1320.
FIGURE 22. *C. petterdi*: lateral teeth showing added ectocone at X3300.
FIGURE 23. *C. petterdi*: lateral teeth at X600 showing elongate basal plates.

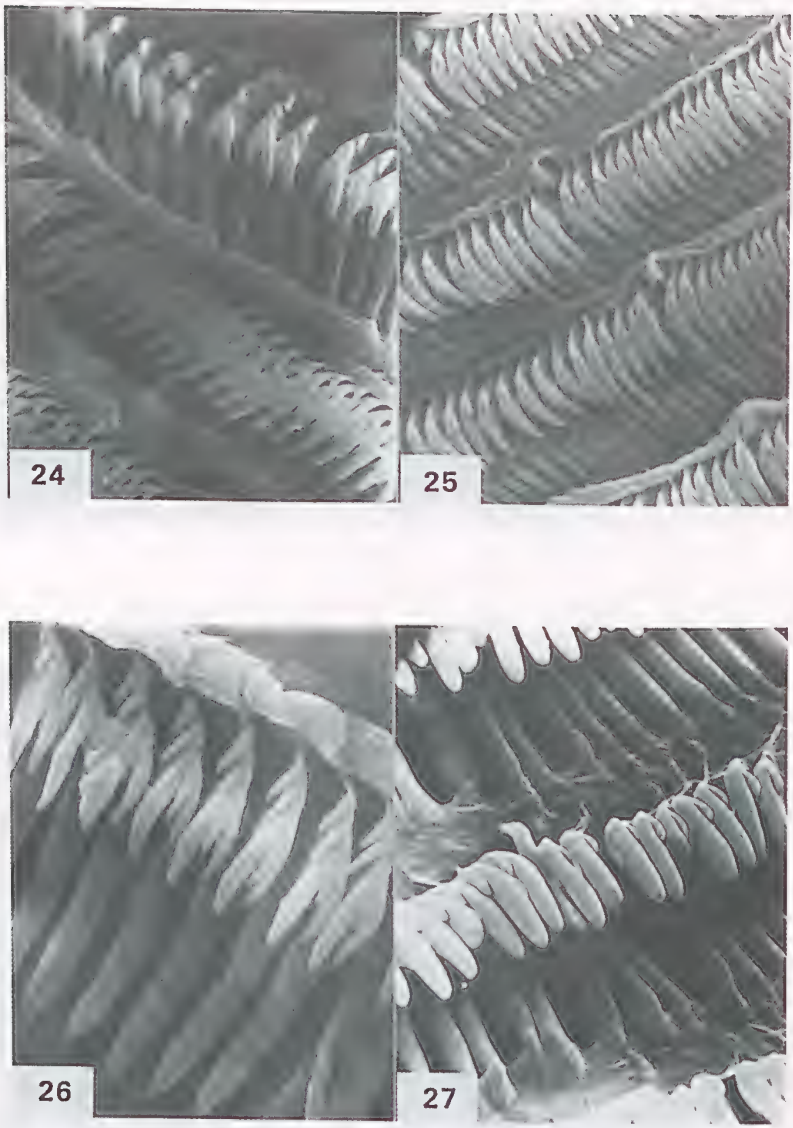


FIGURE 24. *C. petterdi*: latero-marginal teeth at X1500. The additional cusp has become more frequent.
FIGURE 25. *C. petterdi*: transitional teeth at X580 showing an aberrant tooth.
FIGURE 26. *C. petterdi*: marginal teeth at X3000 showing 5 cusps on all teeth and the prominent endocone.
FIGURE 27. *C. petterdi*: strongly worn central and lateral teeth at X3200.

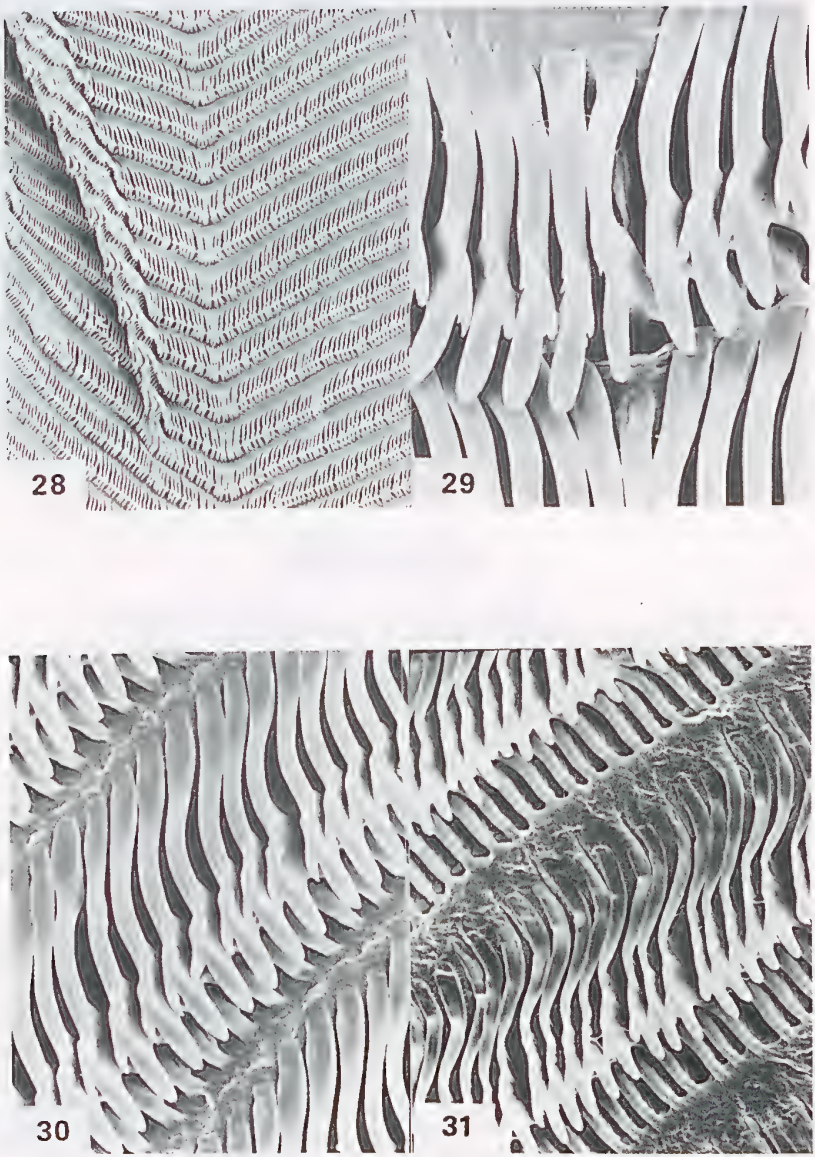


FIGURE 28. *C. bicolor*: radular teeth at X100.
FIGURE 29. *C. bicolor*: central teeth and adjacent lateral teeth at X1000.
FIGURE 30. *C. bicolor*: lateral teeth at X800. Posterior basal plates becoming more exposed.
FIGURE 31. *C. bicolor*: latero-marginal teeth at X800. Basal plates are now curved.

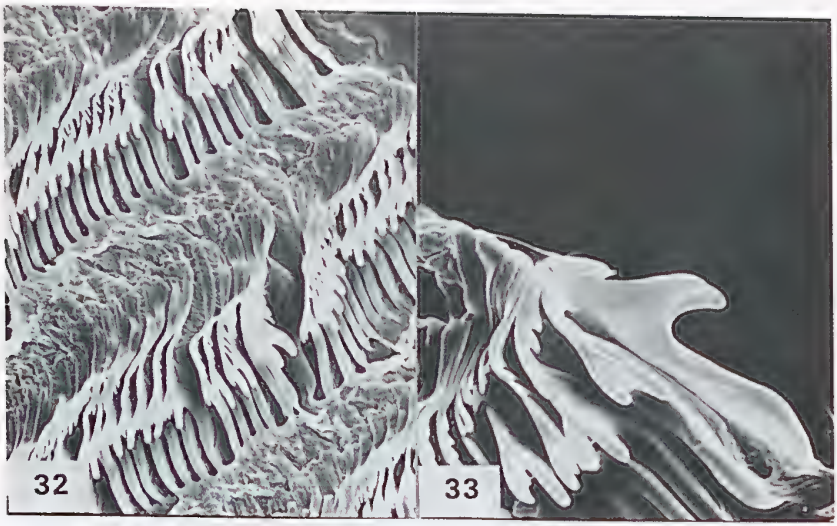


FIGURE 32. *C. bicolor*: marginal teeth at X730. Basal plates curved and twisted.
FIGURE 33. *C. bicolor*: marginal teeth - lateral view at X1800.

ABBREVIATIONS

A- anus;
AL- apical lobe of uterus;
AS- atrial duct sheath;
BD- bursa duct;
BM- buccal mass;
C- crop;
DE- diaphragm epithelium;
E- prostate;
ER- epiphallic pilasters;
G- gonopore;
HG- ovotestis;
I- intestine;
L- lung;
ML- sole margin lobes;
NS- neck skin;
OR- occular retractor muscle;
OV- ovipositor, oviducal pore;
PC- pericardium;
PN- pneumopore;
RM- penial retractor muscle;
SA- salivary gland;
SP- bursa copulatrix;
U- ureter;
VA- vagina;
VE- ventricle

AG- albumen gland;
AP- apical penial process;
AT- atrial duct;
BL- basal lobe of uterus;
BP- bursa duct pore;
CA- carrefour;
DG- digestive gland;
EP- epiphallus;
FO- free oviduct;
GA- genital atrium;
HD- hermaphroditic duct;
K- kidney;
LE- lung tissue;
MP- male duct pore;
O- oesophagus;
OT- occular tentacles;
P- penial chamber;
PG- pedal groove;
R- rectum;
S- stomach;
SC- spermatophore;
T- talon;
UD- uterus;
VD- vas deferens;